8 Linkages between Soil Biota, Plant Litter Quality and Decomposition

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Introduction

In most terrestrial ecosystems, the majority of net primary production enters the decomposition subsystem as plant litter. The breakdown of this litter is determined by a range of factors which each operate at vastly different spatial and temporal scales. In the hierarchical model concept of Lavelle et al. (1993) it is proposed that processes which operate at large spatial scales constrain those which operate at smaller scales; climatic factors help determine abiotic soil characteristics which in turn help determine litter quality and ultimately the activity and composition of soil microbial and invertebrate communities. It is also important to note that there are numerous 'feedbacks' in this hierarchy, with those factors acting at smaller spatial scales also influencing those which operate at larger scales. Thus the effects of plant litter quality on the soil biota regulate the extent to which the biota in turn facilitates the decomposition of plant litter.

Although the microflora is the biotic component that has the enzyme complement most appropriate for the breakdown of plant litter (and is therefore responsible for most of the soil activity: Petersen and Luxton, 1982), it is the nature of biotic interaction between the microflora and soil fauna that is critical in regulating those processes. These interactions broadly occur at three levels of resolution: (i) 'microfood-webs', involving soil nema-todes, protozoa and their predators; (ii) 'litter-transforming systems' involving soil mesofauna and some macrofauna, in which interactions take place in purely organic structures like fragmented material and faecal pellets and (iii) 'ecosystem engineers' involving larger organisms, which interact with microorganisms in both the 'internal' and 'external' rumen, and which build organo-mineral physical structures that significantly alter the habitat for smaller organisms. Predation and competition are often important in regulating the components of the microfood-web system (Wardle and Yeates, 1993) while mutualistic interactions (between gut or soil microflora and soil fauna) become increasingly important for larger organisms, which rely on microbial enzymes to aid digestion of resources (Lavelle, 1994). These interactions are highly important in relation to litter quality: if an organism is regulated by competition (i.e. resource availability) then it is more likely to be regulated by litter quality (bottom-up effects) than if the dominant means of regulation is predation (top-down effects). Mutualistic relationships between microflora and soil fauna are directly related to litter quality, since these interactions are essentially adaptations to the otherwise recalcitrant nature of plant litter.

In this chapter we evaluate linkages between plant litter quality, soil biota and decomposition processes. Specifically we address both sides of the 'Driven by Nature' issue: (i) the effects of quality of

litter input on components of the soil biota; and (ii) the effects of soil biota and their interactions (including adaptive strategies) on patterns of decomposition and nutrient release.

Microflora-Litter Linkages

The lowest trophic level to gain nutrition from plant litter, i.e. the primary saprophytes, consists mainly of two morphologically disjunct groups, the bacteria and the fungi. The mass of these components, or the 'microbial biomass', is very strongly related to resource quality. This is shown by the strong relationships which microbial biomass often demonstrates with soil and litter nitrogen status (Wardle, 1992), by the rapid response of microflora to readily-available carbon sources (Dighton, 1978), and by the negative relationship between the microflora and various compounds such as tannins and 'lignin' (Rayner and Boddy, 1988; Šlapokas and Granhall, 1991). Changes in the microbial biomass during decomposition are usually concomitant with changes in plant litter quality. It has been proposed, particularly for resistant substrates such as wood (Cooke and Rayner, 1984) and some litter types (Wardle, 1993) that as decomposition proceeds the microbial community changes from a disturbed (open) one, to a closed one where microbial competition is most likely to occur, and then to a stressed one (in litter at least this stress appears to emanate from declining pH and exhaustion of key nutrients). Usually microbial biomass is greatest at the closed stage, during which resource competition results in available resources being the most limiting factor (Wardle, 1993).

The species composition of litter fungi is particularly responsive to changes in litter quality. Garrett (1963) proposed a hypothesis of fungal succession in which sugar fungi were followed by those which could degrade cellulose and lignin as the litter quality changed. Although it is now recognized that the mechanisms of fungal succession are much more complex than this, it is still apparent that resource quality does play a role in determining fungal successional patterns. Further evidence for the role of litter quality in influencing fungal species composition emerges when different litter types are compared. For example, Widden (1986) determined that saprophytic fungal community structures strongly mirrored forest vegetation composition, and hence the types of litter input. Similarly Robinson et al. (1994) observed that leaves and internodes of wheat (differing in C-to-N ratio and physical structure) supported vastly different fungal communities. Part of the difference in fungal community structure between litter types is undoubtedly related to differences in the nature of interspecific relationships. Fungi often demonstrate intense competitive interactions, and the most realistic experiments investigating competitive ability (i.e. those on 'real' substrates, not agar) show that competitive balances between different fungal species can depend, quite significantly, on the nature of the resources present (Carreiro and Koske, 1992; Wardle et al., 1993).

Less is understood as to how bacteria respond to litter quality, although they show at least some relationship with changes in quality during decomposition (e.g. Cornejo et al., 1994). However, bacteria are usually associated with aqueous pores in litter and soil, rather than intimately associated with litter as are fungi, and there is both empirical and theoretical evidence that the nature of resources present is less likely to directly affect bacteria than fungi (Wardle, 1995); see below.

If plant litter quality impacts upon the soil microflora, and in particular the fungal component, then it is reasonable to expect that this will in turn determine decomposition rates (Lavelle et al., 1993). For relatively resistant litter types at least this appears to be the case; for example, Flanagan and van Cleve (1983) presented data which indicated that the total mycelial length in organic matter under four different tree species differed considerably, and that this mycelial length was in turn very strongly correlated (r > 0.90) with both N and P mineralization.

Interactions Involving Microfauna

Bacteria are predominantly consumed by bacterial-feeding nematodes (which engulf their prey whole) and protozoa, while fungi are fed upon by fungal-feeding nematodes (which pierce their prey with stylets and ingest their cytoplasmic contents). These microfauna are in turn consumed by top predatory nematodes. The microflora, microfauna, and their predators, comprise the 'microfood-web' system which consists of fungal-based and bacterial-based energy channels (Moore and Hunt, 1988), and in which components may be regulated by competition (through resource limitation, or 'bottom-up' effects) and predation (or 'top-down' effects). Feeding relationships are usually direct, and mutualistic interactions are rare between organisms in adjacent trophic levels.

Using data from an ongoing field experiment, Wardle and Yeates (1993) demonstrated that microbe-feeding nematodes generally did not increase in abundance even when microbial mass was greatly enhanced by resource addition. However, there was a notable increase in top-predatory nematodes, indicative of a tritrophic effect in which the intermediate trophic level (microbe-feeding nematodes) is regulated mainly by top-down effects. It is also apparent from this study, and other data (Wardle, 1995) that, at least in some situations, fungi are resource-limited and respond to resource addition (and are thus likely to benefit by enhanced resource quality) and generally are not strongly regulated by invertebrate grazing pressure, probably because they have the structural and chemical complexity to avoid grazing. Bacteria, meanwhile, that lack the mechanisms to escape grazing to the same degree, are regulated mainly by predation, and do not reach sufficient population sizes for resources to become limiting. Thus, bacteria can enter strong predator–prey relationships with microfauna (Stout, 1980). It would therefore appear that the two components of the microfood-web system which are the most resource-limited, and thus likely to

respond directly to litter quality are the fungi and top predatory nematodes.

Further evidence of this is found in a subsequent study at the same site (Wardle et al., 1995), in which changes in microfood-webs were followed in a sawdust mulch over a 3-year period. Over the first year all groups demonstrated predictable increases as the food web developed. However, even though the N and P content of the sawdust continued to increase over the subsequent 2 years, only fungi and (to a lesser extent) top predatory nematodes showed any response to this enhancement of resource quality; the other groups all instead entered predator–prey cycles with each other which induced substantial temporal variations in population size (Fig. 8.1). These observations also suggest that in the largely aquatic, bacterial-based compartment of this microfood-web system predation becomes increasingly important at lower trophic levels, which is consistent with the hypothesis of Menge and Sutherland (1976), developed for aquatic systems. Meanwhile in the sessile, fungal-based compartment, competition and predation are important at alternate trophic levels, consistent with the hypothesis of Hairston et al. (1960), developed for sessile, terrestrial plant-dominated systems. Our findings of the relative importance of bottom-up and top-down effects in regulating certain components of the microfood-web system (principally nematode groups) are independently confirmed by modelling-based studies (De Ruiter et al., 1995).

We are not suggesting that populations of bacteria and microbe-feeding microfauna do not respond to resource addition and quality. In fact, bacterial-feeding microfauna can show extremely rapid increases with the addition of fresh substrate (Christensen et al., 1992) and respond differentially to the nature of organic matter input from different plant species (Griffiths et al., 1992; Yeates, 1987). However, increases of this sort may be transient and we believe that after resource addition, bacteria and their predators soon enter into predator–prey cycles (Stout, 1980; Wardle et al., 1995)
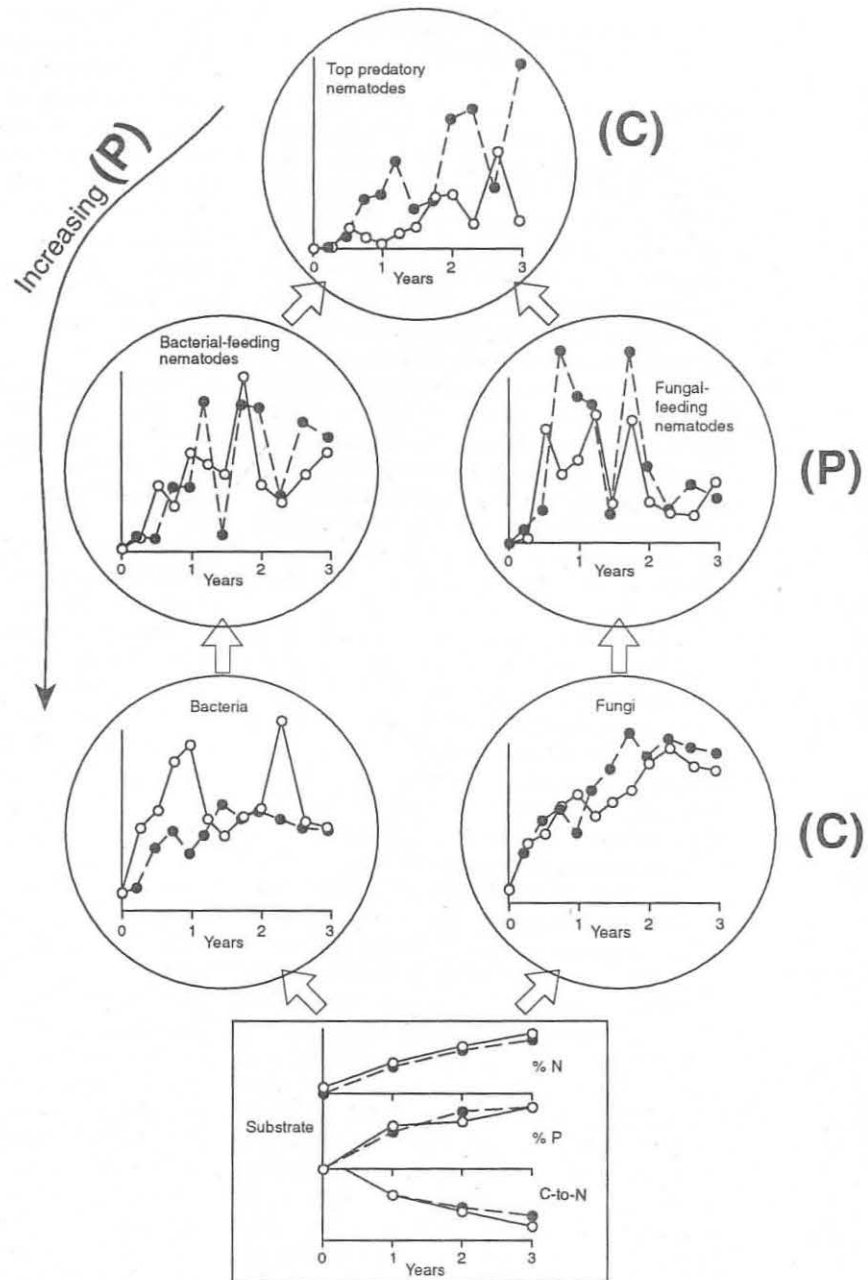
Fig. 8.1. Temporal dynamics of nematode populations, microbial mass and substrate quality in field-placed sawdust. Data presented are relative values, from two sites (represented by solid and dashed lines respectively). After the first year only the fungi show a statistically significant relationship with substrate quality. 'C' and 'P' indicate that competition (resource-limitation) and predation respectively are mainly responsible for regulating each group of organisms. Data derived from Wardle *et al.* (1995).

which are independent of all but relatively large changes in resource quality.

It is the nature of these predator–prey relationships involving bacteria and their grazers which cause them to be of fundamental importance in nutrient mineralization (Clarholm, 1985; Ingham *et al.*, 1985). Bacterial-feeding microfauna enhance nutrient release directly through excretion, and indirectly through maintaining bacteria in a logarithmic growth phase (Trofymow and Coleman, 1982). Griffiths (1994) showed that, over most credible C-to-N ratios of protozoa and bacterial prey, a significant proportion of N ingested by protozoa is likely to be excreted (i.e. 60% if bacteria and protozoa both have a C-to-N ratio of 5). Nutrient status of bacteria (indicative of resource quality) can be very important in determining the degree of mineralization; Darbyshire *et al.* (1994) determined that ammonium excretion by a soil ciliate was significantly enhanced by increasing the nitrogen content of its prey, and that phosphorus was only mineralized when protozoa were fed with bacteria with a high P content. This mineralization is very important in increasing plant growth (and implicitly litter quality), and it has been shown, at least in microcosm experiments, that microfaunal predation enables plant uptake of nitrogen which would otherwise be immobilized in bacterial cells (Kuikman and van Veen, 1989).

Interactions Involving Arthropods

The most intensively studied arthropods in the decomposer subsystem are the springtails and mites. Springtails, cryptostigmatid mites and astigmatid mites are often assumed to be fungivorous and/or saprophagous while many of the components of the Protostigmata and Mesostigmata are assumed to be predatory (see Petersen and Luxton, 1982; Vannier, 1985). However, these distinctions are blurred by omnivory (Wardle, 1995). Although less well understood, larger arthropods may be important both as saprophages (e.g. members of the Isopoda, Formicidae, Diplopoda and Coleoptera) and predators (e.g. members of the Arachnomorpha, Chilopoda and Coleoptera).

Many mesofaunal species, in particular springtails, graze directly on fungal hyphae, although the extent of direct grazing may depend on season and resource quality (Anderson, 1977). Since litter quality determines the nature of the fungal community present (see earlier discussion) it is apparent that this will impact upon those organisms which feed on them. There is strong evidence that springtails selectively graze some fungal species in preference to others (e.g. Visser and Whittaker, 1977) and will actively seek out preferred fungal species over comparatively large distances (Bengtsson *et al.*, 1994). Earlier-colonizing fungi are often eaten in preference to those which colonize later, meaning that grazing of fungi may contribute in part to observed fungal successions (Frankland, 1992). The preference of springtails for earlier-successional fungi (Klironomos *et al.*, 1992) may explain why some springtails dominate earlier rather than later during the decomposition of litter (Wardle *et al.*, 1995). Grazing by springtails also has the potential to benefit fungal production, mainly through dispersal of propagules, removal of senescent hyphae (Visser, 1985) and induction of compensatory growth (Bengtsson *et al.*, 1993), although overgrazing usually proves to be detrimental (e.g. Hanlon and Anderson, 1980). Nutrient concentrations may regulate whether or not stimulatory effects on fungi occur. For example, Hanlon (1981a) found fungal activity to be enhanced by springtails under high substrate nutrient concentrations but reduced by springtails under lower ones; Teuben (1991) found the reverse effect. Therefore these effects do not work in easily predictable directions.

The 'true' saprophagous arthropods, which directly consume litter, fulfil the role of litter transformers. Because of their limited range of enzymes, they are dependent upon microflora for conditioning resources before digestion. This is particularly apparent in litter of very low quality such as wood (Setälä and Marshall, 1994),

and fungal amelioration of wood quality through enzyme activities, improved carbon-to-nutrient ratios, and breakdown of inhibitory compounds appears necessary for subsequent colonization of saprophagous arthropods (Swift and Boddy, 1984). This faunal–microbial association can benefit the microflora considerably due to the fragmentation of litter and reduction of its structual complexity (Tajovský et al., 1992). The transformed litter, in the form of faecal pellets, enhances microbial activity and thus breakdown of the undigested material. This system serves as an 'external rumen', with arthropods reingesting their faecal material so as to reabsorb substrates made available following egestion, and thus optimizing their overall nutrient uptake efficiency. This adaptive strategy is of particular importance in relatively fresh litter with little microbial conditioning, and in nutrient-poor litter; arthropods prevented from reingesting faecal material in such situations can show considerable stress effects (Swift et al., 1979; Hassall and Rushton, 1982).

Although litter-transforming arthropods can induce short-term enhancement of microbial activity, the structures they create can also induce longer-term inhibition of microbial activity and decomposition, through increased compaction, reduced porosity, and less favourable moisture status (Hanlon and Anderson, 1980). This is particularly apparent when the faecal pellets are in the form of small, unstable aggregates (Lavelle, 1994). Reduction of pore size in faecal pellets may result in bacteria being enhanced at the expense of fungi (Hanlon, 1981b).

Litter quality also affects interactions between different faunal groups in the litter transformation and microfood-web systems. For example Tajovský et al. (1992) found that transformation of litter by millipedes caused population increases of both protozoa and nematodes. Interactive effects between faunal groups and litter quality are shown particularly strongly in the study of Coûteaux et al. (1991), in which chestnut leaves were grown in ambient and elevated CO_2, so as to produce leaf litter which differed in quality, principally C-to-N ratio. Addition of nematodes, springtails and isopods all influenced protozoan populations, but these effects were unpredictable and vastly different for the two litter types (Fig. 8.2). A similar pattern emerged in relation to the effects of litter-transformers on nematodes. Since most of these organisms (protozoa, springtails, isopods and most of the nematodes) were of comparable trophic levels (i.e. consumers of microflora and litter) these results suggest that complex competitive and mutualistic relationships exist between different faunal groups, and that changes in plant litter quality can strongly influence biotic interactions (and hence populations of soil organisms) but not in predictable directions.

Litter quality helps determine the ability of saprophagous arthropods to release nutrients. Seastadt (1984) found, upon surveying the literature on short-term experiments, that faunal effects on decomposition and mineralization of nutrients were very variable, and it is likely that this is a function of the nature of the resources present. Teuben (1991) suggested that fungivorous springtails and saprophagous isopods had a buffering effect, both in stimulating nutrient availability and microorganisms in low nutrient conditions, and inhibiting these properties in nutrient-rich conditions. Further data confirming this is presented by Blair et al. (1992) and van Wensem et al. (1993) (and to some extent by Coûteaux et al., 1991, see Fig. 8.2). However, this relationship is probably not universal since stimulation of microflora by mesofauna can also result in nutrient immobilization, reducing nutrient release rates (Seastadt and Crossley, 1980). Blair et al. (1992) concluded that the N-pool of decomposing litter is dynamic with simultaneous mineralization and immobilization occurring; it is the balance between these which will determine the effects that fauna have on decomposition and mineralization, and this is likely to be regulated by litter quality. The effects of arthropods on mineralization are known to significantly alter plant growth, particularly in controlled conditions. In a microcosm system, Setälä and Huhta (1991) found
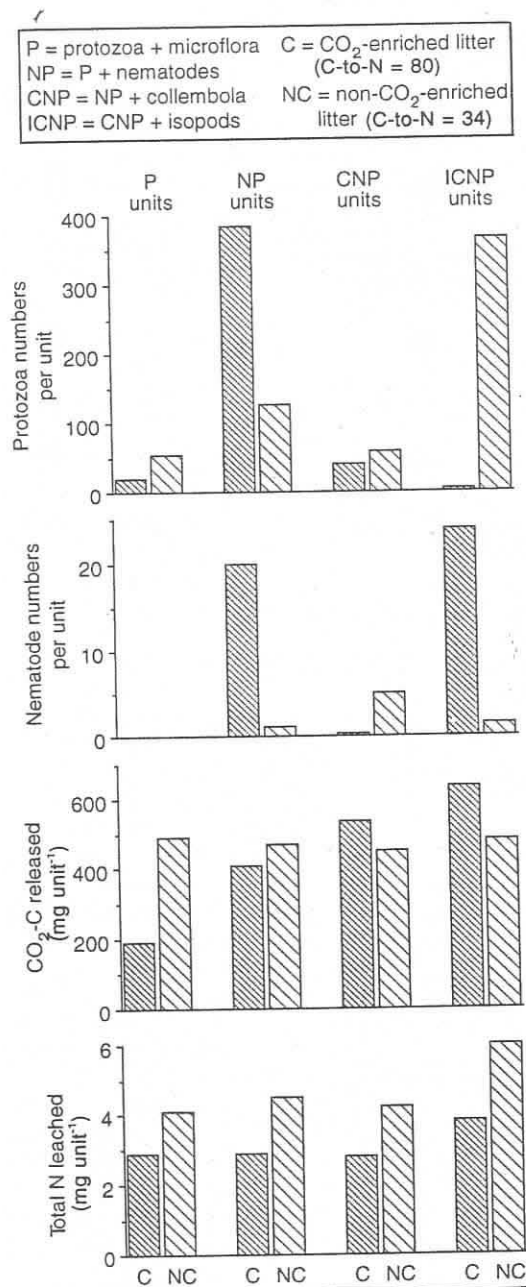
that invertebrates (including arthropods) substantially enhanced both growth and nutrient content of *Betula pendula* seedlings; their results suggest evidence for a positive feedback whereby arthropod feeding activity may potentially improve the nutrient status of subsequent plant litter.

Predatory arthropods consume fauna in both the microfood-web and litter-transforming systems and, although the extent to which they are regulated by litter quality is not well known, any response they show to resource quality is likely to be indirect and related to lower trophic levels (i.e. similar to the trends discussed for top predatory nematodes). However, these organisms do have the potential to exert significant top-down effects, resulting in altered rates of litter breakdown. This is demonstrated in two studies (Santos *et al.*, 1981; Kajak *et al.*, 1993) in which manipulations of predators appear to induce a 'trophic cascade' (similar to those identified in aquatic systems by Carpenter *et al.*, 1988) resulting in an alteration of rates of plant litter mineralization (Fig. 8.3).

Interactions Involving Ecosystem Engineers

Soil invertebrates that can dig soil and produce organomineral structures have been called 'ecosystem engineers' (Stork and Eggleton, 1992; Jones *et al.*, 1994). They comprise the largest soil invertebrates and social insects. When present, they influence the existence of other organisms that are smaller and/or produce purely organic structures, i.e. the litter-transformers, components of 'microfood-webs' and the entire microfloral community (Lavelle, 1994). Ecosystem engineers develop efficient internal mutualistic relationships with microflora which allow them to digest otherwise resistant material. Termites, endogeic and anecic (but not epigeic) earthworms and ants are major components of this group. Some large diplopods, isopods, and even terrestrial crabs that are

P = protozoa + microflora
NP = P + nematodes
CNP = NP + collembola
ICNP = CNP + isopods
C = CO_2-enriched litter (C-to-N = 80)
NC = non-CO_2-enriched litter (C-to-N = 34)

Fig. 8.2. Protozoa and nematode numbers, and C and N mineralization, in chestnut litter of two contrasting qualities, and in response to various faunal additions, after 24 weeks in experimental 'units'. Drawn from Tables 2 and 3 of Coûteaux *et al.* (1991).

TROPHIC CASCADES INVOLVING PREDATORS

(Santos *et al.*, 1981) (Kajak *et al.*, 1993)

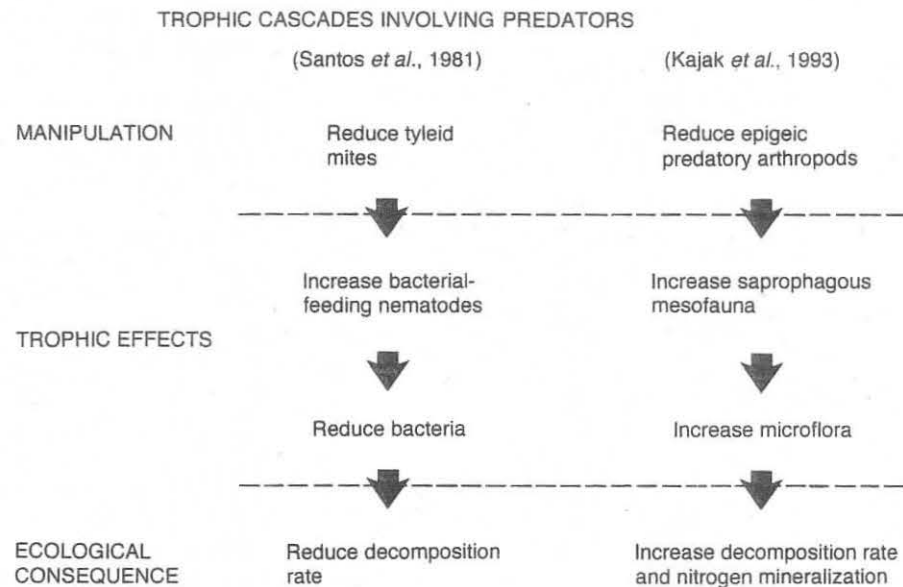|		
MANIPULATION	Reduce tyleid mites	Reduce epigeic predatory arthropods
	▼	▼
TROPHIC EFFECTS	Increase bacterial-feeding nematodes	Increase saprophagous mesofauna
	▼	▼
	Reduce bacteria	Increase microflora
	▼	▼
ECOLOGICAL CONSEQUENCE	Reduce decomposition rate	Increase decomposition rate and nitrogen mineralization

Fig. 8.3. Evidence from two studies for trophic cascades which regulate decomposition of plant litter.

capable of digging burrow systems may be additional components with significant impacts in some situations. These organisms have a very important role in creating habitats for other organisms, and thus serve as excellent examples of 'metabionts' (see Waid, Chapter 11, this volume).

The organisms in this group and their spheres of influence (i.e. the earthworm 'drilosphere' and termite 'termitosphere') are powerful regulators of microbial activity, and hence of decomposition (Lavelle and Gilot, 1994). They are able to digest a number of resistant compounds such as tannin-protein complexes and 'lignin', but they may also be inhibited by the accumulation of certain secondary compounds in litter. Therefore, although their geographic distribution is limited mainly by macroclimate, litter quality is also a relevant determinant of their distribution and activity. These organisms may in turn affect the quality of litter produced, although there is currently little evidence of this in the literature. Further, behavioural and physiological peculiarities of these organisms may profoundly affect the timing and location of decomposition processes.

The quality of litter directly affects its palatability. A number of experiments have shown clear choices by litter-feeding earthworms when given different types of litter (Satchell, 1967; Ferrière and Bouché, 1985). On the same basis termite groups have been classified depending on their preference for dead grass, leaf litter, wood, or 'humus'. In environments where tree species that produce litters of different qualities coexist, earthworm communities may demonstrate obvious patchy spatial distributions. In the Amazon forest of French Guyana, trees may produce litters with highly differing qualities (Charpentier *et al.*, 1995). *Dicorynia guianensis* produces litter with a very high content of polyphenolic complexes which sequester over 80% of litter nitrogen. In contrast, *Qualea* spp. produce litter with low levels of phenolic complexes, but high aluminium levels. The litter which accumulates under *Qualea* trees is favourable for endogeic earthworms which are found at the foot of these trees where they form clearly delineated patches in which litter decomposition is fast, while they are absent from the litter of *D. guianensis* (Fig. 8.4). The litter that accumulates at the base of *D. guianensis* trees is conducive for ingress by plant roots, and a thick root mat develops which

Qualea spp. leaves

Dicorynia guianensis leaves

Endogeic earthworms (detrended)

Roots

% of brown leaves
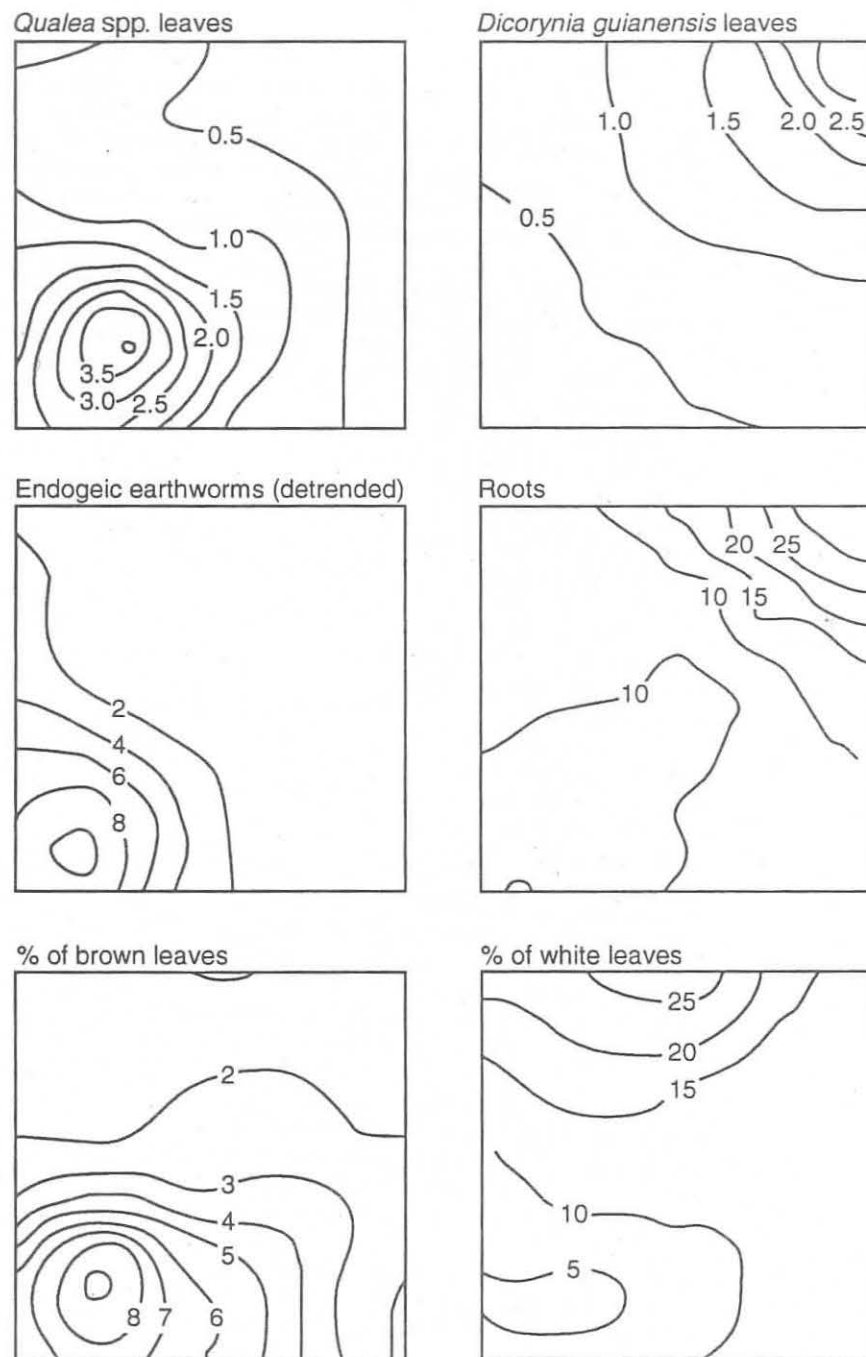
% of white leaves

Fig. 8.4. Spatial distribution of leaves of *Qualea* spp. and *Dicorynia guianensis* in litter, endogeic earthworms, root abundance in soil, brown leaves and white leaves (colonized by white rot fungi) in a 20×20 m plot of tropical rainforest in French Guyana. Numbers on isoclines represent densities m^{-2}.

contains a high proportion of roots of a third tree species, *Eperua falcata*. Such 'single-tree' effects are not uncommon (Boettcher and Kalisz, 1991, 1992) and they may result in the formation of a mosaic of units with rather different decomposer communities and turnover rates of decomposing material.

Following litter deposition, fungal colonization may increase the palatability and digestibility of substrate material. For example, fungus-growing termites can only digest lignocellulosic material after it has been attacked by fungi. These fungi release an enzyme which adds its effects to those of enzymes produced by the termites themselves, allowing digestion of the substrate (Rouland *et al.*, 1990). Anecic earthworms are known to preferentially ingest litter after it has experienced a preliminary fungal attack (Cortez and Hameed, 1988), and some species may accumulate litter around the opening of their burrows forming 'middens' where a preliminary digestion of the 'external rumen' type is observed (Hamilton and Sillman, 1989). Such processes may occur over much larger scales during vegetation succession, e.g. when forests develop, mature, senesce, and develop again. In alpine forests of France, Bernier and Ponge (1993, 1994) found that earthworms which are almost absent during the growing and mature phases of coniferous forest development suddenly appear in units containing senescent and dead trees. At that stage, it seems that spruce litter that accumulates over decades in a moder type of humus suddenly becomes palatable to earthworms. In a few years, a high proportion of this 'free' organic matter is mixed with soil minerals by anecic earthworm activity, and a large flush of available nutrients occurs which is capable of sustaining rapid growth of young forest units. Again, the occurrence of forest patches of different ages, and hence with litter of different qualities, results in a patchy distribution of earthworm populations.

The activities of earthworms and termites may affect litter quality both directly (through improving plant nutrient supply) and indirectly (by influencing vegetation composition in their spheres of influence). As an example of a direct effect, Spain *et al.* (1992) observed in a pot experiment that inoculation of the endogeic earthworm *Millsonia anomala* caused an increase in the concentrations of root nitrogen and phosphorus, and shoot phosphorus of the African fodder grass *Panicum maximum*, as well as changes in the shoot : root ratio. This could be indicative of a positive feedback between root litter quality and earthworm activity. In relation to indirect effects, termites may greatly affect vegetation type through the large structures that they create (Spain and McIvor, 1988). Some termites accumulate nutrients and clay minerals into their mounds thus creating sites with high fertility status. After colony death (which may occur several years or decades after foundation) vegetation invades this soil. Composition of this plant community is specific, and in some East African savannas, these sites are preferentially colonized by shrubs.

Further, ecosystem engineers may affect decomposition processes by transferring litter into structures that they have created. This sometimes results in patchy distributions that are frequently observed in their populations. Sequestration of litter at different stages of decomposition in termite and earthworm structures can also be important in controlling decomposition. For example, coarse organic debris included in compact casts of the endogeic earthworm *Millsonia anomala* had a much slower decomposition rate than similar debris in control, non-aggregated soil (Martin, 1991). Therefore, one year after having been egested by the earthworm, soil had an 11% higher content of this fraction despite the partial digestion that had occurred during transit through the earthworm gut.

Above-ground Associations: Invasive Plants, Biodiversity and Herbivores

The relationship between plant litter quality and decomposition are ultimately

large spatial scales, including those relating to the nature of the plant community present (c.f. Lavelle *et al.*, 1993). Grime (1979) proposed a theory in which plants growing in communities could be classified as according to three main strategies, namely 'ruderals' (adapted to disturbed sites), 'competitors', and 'stress-tolerators' (adapted to non-varying, harsh conditions). This is relevant in terms of litter quality; ruderals produce litter with a high nutrient status and few secondary metabolites while stress-tolerators produce nutrient-poor litter with high concentrations of secondary metabolites (Hobbie, 1992). The ecological consequences of strategy-induced effects can be demonstrated through two examples involving invasion by plants with vastly different strategies. The first example involves the invasive pasture weed *Carduus nutans* in grasslands dominated by *Lolium perenne* and *Trifolium repens* in the Waikato area of New Zealand (Wardle *et al.*, 1994). This species has a ruderal strategy, and establishes as randomly-located individual plants, usually as a result of local disturbance. Its litter has a high nitrogen content (3.5%) and decomposes extremely rapidly (half-life = 15 days). The litter is clearly favourable for soil biota: the microbial biomass, springtail populations and epigeic arthropod populations are, respectively 1.2, 3-and 1.5-fold greater in patches with *C. nutans* litter than in adjacent pasture. C. *nutans* thus induces random patches of temporarily enhanced biological activity on an otherwise relatively invariant landscape. The second example involves the invasive ericaceous dwarf shrub *Empetrum hermaphroditum* in the Swedish boreal forest. This plant is highly stress tolerant and invades late successional systems as randomly-located clones (Zackrisson *et al.*, 1995). It produces high concentrations of secondary metabolites, and is highly allelopathic, providing one of the few unequivocal examples of allelopathy in the literature (Nilsson, 1994). The decomposition rate of *E. hermaphroditum* litter in microcosms is around 77% of that of the other dominant ground-dwelling shrub present, *Vaccinium myrtillus* (Wardle, Nilsson and Zackrisson, unpublished). Further, the decomposition rate of litter of various species placed in *E. hermaphroditum* humus is only 70% of that placed in *V. myrtillus* humus. This appears to reflect the negative effects of *E. hermaphroditum* on the soil biota: microbial biomass in *E. hermaphroditum* humus is only 60% of that in *V. myrtillus* humus, and soil macrofauna is almost completely absent. As a result, invasion by *E. hermaphroditum* results in thick humus layers, with long term effects on nutrient availability and the soil biota; for example, in humus profiles, layers with high pollen counts of *E. hermaphroditum* (indicating that the humus is of *E. hermaphroditum* origin) show suppressed microbial activity relative to layers with low *E. hermaphroditum* pollen even 1000 years following formation. Invasion of *E. hermaphroditum* is reversed by wildfire, and this is at least partially attributable to adsorption of inhibitory compounds by newly produced charcoal (Zackrisson *et al.*, 1996). Thus when the natural fire-cycle is interrupted, *E. hermaphroditum* has the potential to induce general decline of the boreal forest ecosystem.

An extension of these individual-species effects are multiple-species effects. There has been considerable recent interest in the effects of plant species richness on ecosystem function (e.g. Vitousek and Hooper, 1993), although the ideas have actually been expressed considerably earlier; Odum (1969) speculated if diversity could alter physical stability in the ecosystem, and whether species richness was 'a necessity for long life of the ecosystem'. These ideas are directly relevant to plant litter quality: the majority of net primary production enters the decomposition system as litter, and if such a hypothesis is correct then species richness of plant litter would be expected to have important ecological effects. Although litter diversity may be an important component of litter quality, this aspect has received little attention to date. This hypothesis can be tested using 'litter-mix' experiments, in which the effects of mixing litter of different species are compared with what would be expected based on the effects of the
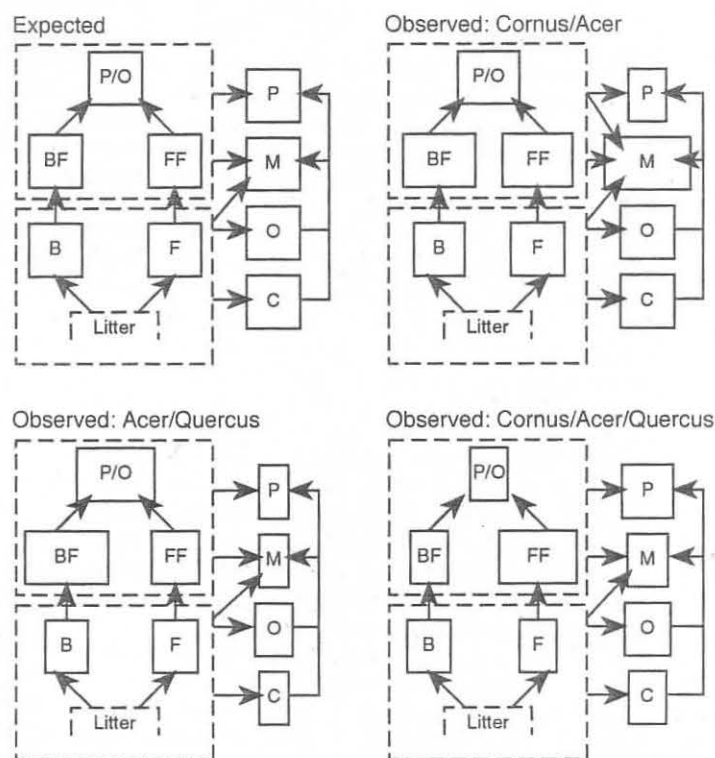
Fig. 8.5. Effects of litter diversity on microbial and faunal components of the detritus food-web in forest ecosystems. For each functional group the area of each rectangle represents the observed mass or population of that component in the two- or three-species litter mixes, relative to the expected values derived from litter monocultures, assuming effects of all litter-types are purely additive. Symbols: B = bacteria; F = fungi; BF = bacterial-feeding nematodes; FF = fungal-feeding nematodes; P/O = predatory/omnivorous nematodes; C = Collembola; O = oribatid mites; M = mesostigmatid mites; P = protostigmatid mites. Calculated from data presented by Blair *et al.* (1990).

components in monoculture. Chapman *et al.* (1988) observed, in considering litter in monoculture and mixed stands of four tree species, that mixture effects were often different from that expected based on the monocultures, but these effects were not predictable. Specifically, in a mixed *Pinus sylvestris – Picea abies* stand microbial activity, nutrient mobilization, and populations of springtails and earthworms were greater than expected, while in *P. abies – Alnus glutinosa* and *P. abies – Quercus petraea* mixes microbial activity and nutrient mobilization were less than expected. In their study, biodiversity of

litter input therefore altered ecosystem function but not necessarily always in the same direction. Blair *et al.* (1990) evaluated decomposition processes and components of the soil biota, in litterbags containing monocultures, and two- and three-species mixtures of *Acer rubrum*, *Cornus florida* and *Quercus prinus*. Decay rates of mixed litter did not differ from what was expected based on monoculture values, but nitrogen release in the mixtures was greater than expected in the initial phases of the study. These differences in mineralization appeared to be related to differences in the abundances of decom-

poser organisms. For example, fungivorous nematodes and mesofaunal groups were respectively generally greater and generally lesser in the mixtures than what would be expected based on the monocultures (Fig. 8.5). Results from Blair *et al.* (1990) indicate that litter biodiversity may affect different pools of soil organisms but not in easily predictable directions. Wardle *et al.* (1996) conducted a litterbag study in which mixtures of between two and eight species (together with appropriate monoculture litterbags) were randomly generated from a pool of 32 plant species (including grasses, herbs and trees), so as to evaluate whether decomposition, nitrogen mineralization and litter microbial biomass were affected mainly by species richness or mainly by the degree of dissimilarity of different litter types. Their results showed that species richness of litter may have either positive or negative effects on these properties, depending upon the types of plants considered. Further, while increasing diversity from one to two species had detectable effects, there was no consistent effect observed of increasing species richness from two to eight species, indicating that considerable species redundancy exists in relation to the ecological effects of litter diversity. There is also evidence that plant litter decomposition can be altered by plant species diversity in controlled experimental conditions (Wardle and Nicholson, 1996) although again, these effects do not work in predictable directions.

Finally, above-ground trophic diversity also impacts upon litter quality. Foliar herbivory can substantially alter litter quality and hence soil organisms. This can happen in two ways, with vastly different consequences. The first involves herbivores inducing a shift in the plant's chemistry and hence quality of litter return. Thus, herbivores have often been shown to stimulate decomposer organisms (e.g. Ingham and Detling, 1984; Seastadt *et al.*, 1988). These effects are probably partly due to enhancement of nitrogen status of root litter produced by grazed plants (Seastadt *et al.*, 1988), although grazing optimization of root productivity and

herbivore-induced root mortality (and associated resource-input) may also contribute (Merrill *et al.*, 1994). The second involves herbivores preferentially grazing some plant species, allowing others to dominate. The preferentially eaten plants are also those with superior litter quality, so the community becomes dominated by plants with poor litter quality. This effect is demonstrated by Pastor *et al.* (1988; 1993), who found that selective browsing by moose of aspen, poplar and ash (all with high litter quality) allowed spruce (with poor litter quality and a high cellulose content) to dominate. The net result is a lower soil microbial biomass, lower decomposition rate and less nitrogen mineralization, and ultimately retarded development of the soil profile.

Conclusions

Plant litter quality is of critical importance in regulating both the soil biota and the nature of soil biotic interactions, and these effects operate at three different scales of resolution; the 'microfood-web' system, 'litter-transformer' system, and the system involving 'ecosystem engineers'. These systems are constrained by the input of plant litter, which is in turn determined by the nature of the plant community. Although in any plant community there are usually several types of litter being returned to the soil, the effects of litter diversity on the soil biota and biotic processes has been largely unexplored; there is, however, evidence that litter diversity effects do not work in predictable directions, and that there may be considerable species redundancy. The importance of plant litter input in determining soil biological interactions is also apparent in studies which have considered the effects of spatial placement of plant litter (and consequently spatial heterogeniety), and those which have considered changes in components of the decomposer system (including humus dynamics: Bernier and Ponge, 1994) during vegetation succession. Ultimately the 'Driven by Nature' issue involves two components,

biota, and the effects of biotic interactions on soil ecological processes, and an understanding of both components is essential in understanding the ecological effects of plant litter quality.

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